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Heavy Metal Toxicity in Plants: An Overview on Tolerance Mechanisms and Management Strategies

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ABSTRACT

Heavy metals are one of the factors that pollute the environment and significantly affect soil fertility, plant physiology, development, and productivity. The tolerance of plants to toxicity depends on the species and tissue, element type, and duration of exposure to stress. Some special signal molecules such as nitric oxide (NO), hydrogen peroxide (H_2O_2), beneficial ions, hyperaccumulating plants, stress hormones, nanoparticles, organic compounds, and microbial applications can be recommended to alleviate the stress effects caused by toxic heavy metals in plants. Induction of other promising techniques like seed priming, active involvement of plant growth regulator, use of osmoprotectants, successful plant microbes' crosstalk and recent utilization of nanoparticles are worth using strategies in mitigation of heavy metal stress in plants. These practices effectively regulate the activities of antioxidant enzymes for the alleviation of stress in plants, creditably improving the plant tolerance via preserving cell homeostasis and amending the adversative effects of heavy metal stress in plants. These inventive strategies offer an enriched understanding of how to boost crop productivity under heavy metal stress in order to decrease the risk to global food security.

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Introduction

Heavy metals, the elements with a specific gravity higher than 5 (g cm^{-3}) (Khanna et al., 2018), at low concentrations, are vital for plant growth and development. These metals include aluminum (Al), arsenic (As), cadmium (Cd), cobalt (Co), chromium (Cr), copper (Cu), iron (Fe), mercury (Hg), manganese (Mn), nickel (Ni), lead (Pb), molybdenum (Mo), and zinc (Zn). These metals at higher concentrations are toxic to the environment (Luo et al., 2020) as well as to animals and plants. Heavy metals, when occurring at low concentrations, are involved in redox reactions, electron transfers, nucleic acid metabolism, and as an integral part of several enzymes. Some heavy metals such as Cu, Fe, Mn, Zn, and Ni are components of some enzymes and proteins, thereby essential for plant growth and metabolism. Plants, when grown in soils contaminated with heavy metals, are often faced with some changes at physiological levels which included nutrient accumulation, respiration, and gas changes. Heavy metals at higher concentrations also affect plant metabolism and physiological events, reduce growth, and contaminate the environment. Heavy metals also cause oxidative stress in plants mainly through the excessive production of reactive oxygen species (ROS). Excessive production of ROS increases the production of unsaturated lipid peroxidation fatty acids and disturbs cell membrane function. Cell membrane damage can cause an imbalance in enzymatic activities, disrupts the normal redox balance of the cell, and causes oxidative damage when affects cell metabolism (Luo et al., 2020). Metals accumulation in plants significantly affected plant viability, carbohydrate level, and respiratory rates (Kumar et al., 2019).

Heavy Metal Resistance (HMR) in Plants

Plants have developed some mechanisms against heavy metal stress. These mechanisms include immobilization, exclusion of plasma membranes, restriction of absorption and transport, synthesis of specific heavy metal carriers, induction of stress proteins, chelation, and sequestration by certain ligands (Kumar et al., 2019; Yu et al., 2019; Luo et al., 2020).

Resistance Mechanisms

Root Exudates

Root secretions are grouped as high molecular weight (polysaccharides and proteins) and low molecular weight (ie amino acids, organic acids, sugars, phenolics) compounds (Bais et al., 2006). Among these, low molecular weight organic acids are the most abundant and reactive with metals (Koo et al., 2010).

Organic Acids

Organic acids have one or more carboxyl groups and can be chelated with heavy metals. Thus, non-toxic compounds are formed by preventing them from entering the plant. The secretion of organic acids such as oxalic acid (OA), citric acid (CA), malic acid, tartaric acid, and succinic acid increases under heavy metal stress. It has been observed that the total organic acid secretion is higher in stress-resistant paddy varieties under Cd stress (Fu et al., 2017). Similarly, it has been found that the roots of Cd-tolerant peppers have more tartaric acid, oxalic acid, and acetic acid (Xin et al., 2014). Saber et al. (1999) stated that malic and citric acids may play a significant role in inducing resistance in *Helianthus annuus* (L.) to heavy metals. Previous research on Pb stressed *Larix olgensis* seedlings demonstrated that oxalic acid or citric acid ameliorated Pb-induced physiological toxicity (Song et al., 2018).

Amino Acid

Amino acid secretion increases in plant roots under heavy metal stress conditions. The secretion of amino acids, including methionine, lysine, and histidine, from the roots increases significantly in paddy rice under Cd stress (Wang et al., 2016). Amino acids secreted from the roots are providing a food source for bacteria, fungi, yeast and sulphur bacteria. Sulphur bacteria also prevent heavy metals from entering the plant by reacting with heavy metals. Sharma and Dietz (2006) revealed that histidine, other amino acids, and particularly phytochelatins and glutathione play a role in metal binding. Free amino acids such as histidine and nicotinamide play an important role in heavy metal hyperaccumulation (Hassan and Aarts, 2011).

Soluble Sugar and Protein

Soluble sugar is an important component produced by plants during respiration and photosynthesis (Aldoobie and Beltagi, 2013). The first of these is their involvement in various metabolic events; the other is that they act as signal molecules that regulate different genes specifically involved in photosynthesis, sucrose metabolism, and osmolyte synthesis (Rosa et al., 2009). Under heavy metal stress, more accumulation of soluble proteins and sugars is maintained in the plants (Yu et al., 2019). The soluble sugar content increases with increasing heavy metal concentration (Guangqiu et al., 2007).

Subcellular Structure

Cytoderm

Cellulose, hemicellulose, pectin, and proteins provide structure to the cell wall. Some of these functional groups such as carboxyl, hydroxyl, amino, and aldehyde groups prevent heavy metals to enter the cell. After removal of hemicellulose from the root zone in cabbage, leaf lettuce, pepper, tomato, and rice plants, zinc accumulation in cytoderm decreased significantly and increased in shoots (Choi and Harada, 2005). It has been observed that the application of NO increases the hemicellulose and pectin content in the cytoderm in some plants and increases the tolerance of the plants to Cd stress (Gilliam et al., 2016). It is observed that in cotton plants under stress, the cytodermin and the Casparian strip are thickened, thus the transport of Cd ions is blocked, and toxicity symptoms are alleviated (Chen et al., 2019).

Cytomembrane

It has been observed that overexpression of *OsHMA3* increases the tolerance of paddy roots to cadmium (Sasaki et al., 2014), but overexpression of *NtHMA3a* and *NtHMA3b* did not increase mercury tolerance in tobacco, *ABC* carriers played an important role (Chang and Shu, 2015). Similarly, overexpression of *PtABCC1* has been observed to increase Hg tolerance in various plants (Sun et al., 2018).

Chelation

Amino acids form a strong affinity for metal ions such as histidine, Zn^{2+}, Co^{2+}, Ni^{2+} and Cu^{2+} and therefore are involved in the direct chelation of heavy metals. When there is a high accumulation of cadmium in the cell wall, cadmium is transported to the vacuole. Cadmium combines with proteins, organic acids, sugars and other organic substances in the vacuole to form macromolecular compounds through chelation, thereby reducing cadmium toxicity (Riyazuddin et al., 2021; Yang et al., 2021).

Metallothionein (MT)

Metallothionein (MT) is a low molecular weight, cysteine-rich, metal-binding protein that is directly synthesized by mRNA transcription caused by heavy metal stress. Metallothionein is known to play a protective role against the toxicity of heavy metals and reactive oxygen species (Sato and Kondoh, 2002). The *MT* gene has been cloned in pea (Evans et al., 1992), mustard, and tobacco (Andrews and Geiser, 1999). In Arabidopsis, the *MT2* gene has been found to increase tolerance to zinc (Gong et al., 2009), while the transfer of the *SaMT3* gene to *Escherichia coli* increases resistance to Cu and Pb (Gupta et al., 2013a).

Phytochelatins (PC)

Phytochelatins can bind to a variety of metals, including Cd, As Cu or Zn, through sulfhydryl and carboxyl residues, but biosynthesis is controlled by metal Cd or metalloid As. With the overexpression of phytochelatins synthase genes, Cd tolerance increases in yeast and bacteria (Gupta et al., 2013a). Cadmium, copper, mercury, lead, zinc, silver, strontium, gold, tin, nickel, arsenic, and selenium can cause phytochelatins production in maize and wheat. Different heavy metals have different bonding states to the phytochelatins. Cadmium has the strongest binding ability, followed by lead, zinc, antimony, silver, mercury, arsenic, copper, tin, gold, and strontium (Grill and Zenk, 1985).

Reduced glutathione (GSH)

It is an amino acid derivative composed of reduced glutathione, glutamic acid, cysteine, and glycine. It can also act as a ligand to chelate heavy metals and reduce the toxicity of heavy metals. Reduced glutathione application promotes the formation of phytochelatin in some plants, causing it to reduce cadmium toxicity (Ding et al., 2017). Under conditions of HM stress, reduced glutathione helps reduce ROS levels to maintain proper cellular homeostasis (Asgher et al., 2017).

Strategies for Heavy Metal Tolerance in Plants

Several strategies have been opted to mitigate the detrimental effects induced by the heavy metal stress. Strategies that are used for the successful mitigation of heavy metal stress are given below.

Seed Priming

Heavy metal stress undesirably affects all phases of the plant from seed germination to the full growth of the plant, eventually, decreasing the overall yield of the economically vital crops. Sowing of seeds in soil that is excessively contaminated with toxic heavy metals results in declined germination, lowered growth of roots and shoots, fewer plant seedlings, and reduced biomass production. Metals are necessary for plant growth, but when they are present in excess amount, it causes severe toxicity and hindered the growth of the plant (Aihemaiti et al., 2018). In plant growth, seeds have a vital role as every crop is grown from the health seed. However, occasionally it experiences soil toxicity that limits the seedling emergence and ultimately leads to insignificant growth of the plant (Bisen et al., 2015). Plants developed various mechanisms to survive the heavy metal stress effectively (Emamverdian et al., 2015). Seed priming is considered as the most important instant approach to mitigate the adversarial effects of heavy metal stresses on plants as reported in different studies (Shah et al., 2020; Basit et al., 2021; Chen et al., 2021). Seed priming is denoted as a physiological strategy of seed hydration used to improve the metabolic process in plants to fasten the rate of germination, growth of plant seedlings as well as crop yield under both biotic and abiotic stress conditions (Rhaman et al., 2020).

Seed priming upholds a momentary balance of ROS scavengers to alleviate the oxidative stress produced under stressful conditions (Hussain et al., 2017). It results in the decreased production of hydrogen peroxide and malondialdehyde and improves the concentration of proline (Hossain et al., 2015). Plants accumulate inactive signalling proteins in primed seeds. These inactive proteins become active soon after sensing the stressful conditions (Saboor et al., 2019). Priming boost the vitality of the plant seed (Afzal et al., 2013). Different priming agents are used in this technique like salicylic acid (SA) which is actively involved in the regulation of various physiological changes under stressful conditions (Fariduddin et al., 2018). Salicylic primed seeds of *Trifolium repens* (perennial) and *Trifolium vesiculosum* (annual) showed significant improvement in germination and seedling growth of these two species against Al stress (Bortolin et al., 2020). Similarly seed priming with salicylic acid (SA) and sodium hydrosulphide (NaHS) significantly improve the lead tolerance in *Zea mays* L. through a reduction in the uptake of Pb, thus resulting in dropping Pb toxicity to the food chain (Zanganeh et al., 2020). Selenium (Se) primed seeds of rice enhanced the growth and yield of the plant by restricting the translocation of arsenic (As) to the aerial parts of the plant. Full-grown plants of primed seeds showed much higher height and enough biomass under arsenic stress, signifying that seed priming is effective for enhancing plant growth against arsenic stress (Moulick et al., 2018). This overwhelming functioning of seed priming against heavy metals stress along with its positive effects on germination, growth, and yield of the different crops worldwide is quite evident as depicted in Table 1.

Plant Growth Regulators

Plant growth regulators (PGRs) are known as synthetic and naturally occurring compounds that directly affect the all-important metabolic processes and development in higher plants, generally at small doses. Plant growth regulators directly affect the hormonal status of the plants, and are not phytotoxic. They don't possess any nutritive value for the plant (Rademacher, 2015). Plant growth regulators has the capacity to govern the majority of plant growth parameters from seed germination to reproduction and finally to plant death (Bhardwaj and Kapoor, 2019). Major PGRs including plant hormones like cytokines, auxins, jasmonic acid, abscisic acid, ethylene, gibberellins, and salicylic acid have attained significant attention over the last few years by agronomists as a suitable media for sustainable growth and development of plants under stressful conditions (Asgher et al., 2015). Use of different PGRs is regarded as an appreciated approach for the promotion of effective crop production (Nazir et al., 2019a, b).

Implementation of PGRs approach for the remediation of heavy metal stress is a very effective tool as reported in previous studies (Sytar et al., 2019; Aftab and Hakeem, 2021; Ranjan et al., 2021). Abscisic Acid (ABA) is a very important hormone that regulates the uptake of heavy metals in plants. Tang et al. (2020) studied the effects of various concentrations of abscisic acid on uptake of cadmium in lettuce under cadmium stress. Results indicates that the foliar application of abscisic acid (ABA) considerably improves the overall biomass of the plant and reduced the Cd concentration in shoots of the lettuce plant by 23.60 % as compared with the treatment of Cd. Thus, restricting the accumulation of toxic Cd concentration in edible parts of the plant. Similarly in another study, exogenous application of ABA also restricts the accumulation of Cd in *Arabidopsis*, increased the growth, and improved the photosynthesis under Cd stress (Pan et al., 2020). Salicylic acid (SA) is another plant hormone involved in affecting the growth of plant, developing and creating resistance in plants against various stressful conditions. Salicylic acid performs a vital role in the photosynthetic cycle, ion channel regulations, and improves the defense mechanism of plants by increasing activities of various antioxidant enzymes (Pan et al., 2015). Exogenous SA application effectively mitigated the Cd stress by stimulating the antioxidant enzymatic pathways via improving the endogenous SA contents, relative water content, proline and chlorophyll content together with a considerable decline in hydrogen peroxide (H_2O_2), superoxide anion radicals (O_2^-) and malondialdehyde (MDA) in tomato plants exposed to Cd stress (Li et al., 2019).

Different studies reported that the application of gibberellins (Gas) reduce the harmful effects of abiotic conditions, especially heavy metal stress. Gibberellins perform crucial role in improving the cell division, cell elongation and are effectively involved in the expansion of different transition phases in plant life. Chen et al. (2021) studied that the application of gibberellins (10 μM) depleted the detrimental effects of Cd stress on plant growth. Its application significantly reduced the Cd absorption and translocation from roots to shoots in lettuce plant. Furthermore, gibberellins diminish the damaging effects of copper in spinach seedlings by increasing the concentration of proline and activities of antioxidant enzymes (Gong et al., 2021). Jasmonic acid (JA) is signaling molecule involved in governing of cellular defense and sequential developments in plants (Gomi, 2021). It plays a very significant role in controlling various stress responses during the developmental phases of plants (Liu and Timko, 2021). Kamran et al. (2021) reported that exogenous application of JA (0, 5, 10, and 20 μM) offset the deleterious effects of chromium stress on the physiology and growth of the choysum plant. Jasmonic acid application improves the photosynthetic efficiency and nutrients homeostasis in Cr stressed choysum plant. Its application mitigated the oxidative stress induced by the Cr stress via regulating glyoxalase defense and antioxidant system in the plant. Thus, it is concluded that these plant growth regulators improve plant tolerance against heavy metal stress. Recent studies indicating the aptitude of different plant growth regulator (phytohormone) to mitigate heavy metal stress in different plants species is given in Table 2.

Osmoprotectants

Plant employs different approaches to avoid heavy metal stress. One such approach is the utilization of osmoprotectants (Zulfiqar et al., 2020). Osmoprotectants are very small, highly soluble, and electrically neutral molecules with low toxicity. They are also known as compatible solutes as they possess high solubility and little interference with metabolic pathways. They include polyamines (Putrescine, Spermidine, Spermine) amino acid (proline) betaines (glycine betaine), Carbohydrate (Threalose, Fructan), and Sugar alcohol (Inositol) (Brito et al., 2019). These compatible molecules efficiently accumulate in plants when growing situations are not appropriate for plant growth and development. They are accountable for preserving the internal physiological practices that guarantee plant subsistence under prime conditions (Yang and Guo, 2018; Seleiman, 2019). These compounds are used for seed treatment or applied exogenously to protect the subcellular structures and to increase the activities of antioxidant enzymes in plants (Yang and Guo, 2018). These compounds are typically used during seed treatment or exogenously applied during various stages of crop development.

Among these compatible molecules, proline is regarded as the most proficient molecule that is produced in various plants under adverse environmental conditions (Siddique et al., 2018). Effective role of proline against heavy metal stress is extensively reported in different studies (Rasheed et al., 2014; Konotop et al., 2017; Yu et al., 2017). Proline takes active part in osmotic adjustment of various plants to increase plant resistance to mitigate the oxidative stress produced by the heavy metal stress via scavenging of ROS (Adejumo et al., 2015). They reported massive improvement in growth and increase tolerance in maize plant against stress induced by lead. Similarly exogenous application of proline effectively alleviated the serious oxidative stress produced by the higher accumulation of Cd in olive plants. Application of proline improves the antioxidant system, photosynthetic activity, nutritional status, and growth of the plant under Cd stress (Zouari et al., 2016). Proline application helps to stabilize the protein structure, improve content of chlorophyll, stimulate the antioxidant enzymes, and perform a multifunctional role in plants to mitigate heavy metal stress as given in Figure 1.

Comparable to what we have noticed above, glycine betaine also reported to mitigate the heavy metal stress in plants. Being more metabolically stable among other osmoprotectants like sugar and proline, glycine betaine is more useful (Jain et al., 2021). Glycine betaine is important osmoregulator in plants. Application of glycine betaine (GB) improves growth and development of the plant, increase nutrients uptake, reduce the oxidative stress via limiting the uptake of heavy metals in plants (Ali et al., 2020). Glycine betaine under heavy metal stress improves plant growth via improving the chlorophyll content and minimizing oxidative damage (Demidchik, 2015). Similarly, Ahmad et al. (2020) also reported that application of GB maintains and improves plant growth, biomass production, gas exchange parameters and photosynthetic traits in *Brassica oleracea* L by overcoming the oxidative stress induced by chromium stress. Application of GB showed a useful impact in inhibiting the contents of lead in tissues of olive plant, thus reducing its unapproachable influences on plant growth (Zouari et al., 2018)

Soluble sugar molecules such as trehalose, hexose, and sucrose act as osmoprotectants. They perform a vital role in the maintenance and conservation of cellular organizations, scavenging of ROS and improvement of photosynthetic proficiency. They perform various physiological functions such as coordinating antioxidant activity, consolidating membrane integrity, and sustaining water requirements under stressful conditions (Ahmad et al., 2020). Trehalose (TR) plays a vital role in osmotic protection, thus improving plant tolerance toward heavy metal stress. Wang et al (2020) studied that the application of TR effectually decreased the toxicity of harmful CD to rice plants by creating TR-CD chelate. Exogenously applied TR restricts the accumulation of harmful concentrations of CD in roots and shoot of the rice seedlings.

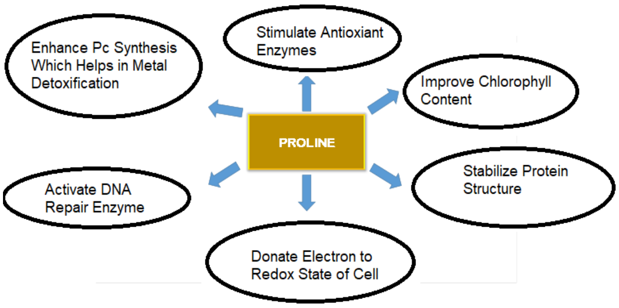

Figure 1. Multiple functions of proline under heavy metal stress.

Table 1. Seed priming with different agents for mitigation of heavy metal stress

HMS	Plant species	Priming agent	References
Cd	Black Cumin (Nigella sativa)	salicylic acid (SA)	Espanany et al. (2016)
Nano -ZnO	Rice (Oryza sativa)	polyethylene glycol	Sheteiwy et al. (2016)
Cd	Lettuce (Lactuca sativa L.)	salicylic acid	Šabanović et al. (2018)
Cd	Lettuce	Silicon	Pereira et al. 2021
Pb	Wheat (Triticum aestivum)	Purslane extract, Aqueous chard extract	Sobhy et al. (2019)
Cd	Maize (Zea mays)	Multiwall carbon nanotubes (MWCNTs)	Chen et al. (2021)
Cd	Faba bean (Vicia faba)	Calcium chloride	Nouairi et al. (2019)
Mn	Sunflower (Helianthus annuus L.)	Sulfur Nanoparticles	Ragab & Saad-Allah (2020)
Cd	Cucumbers (Cucumis sativus)	3-epibrassinolide	Shah et al. (2020)
Cr	Rice (Oryza sativa)	Brassinosteroids	Basit et al. (2021)
Cd	Coriandrum sativum	Karrikinolide	Sardar et al. (2021)
As	Garden cress (Lepidium sativum)	Gibberellic acid (GA), Salicylic acid (SA), Citric acid (CA), Sodium chloride (NaCl), Potassium chloride (KCl), Zinc (Zn) and Iron (Fe)	Nouri & Haddioui, (2021)
Cd	Cowpea (Vigna unguiculata (L.)	Proline and Glycine Betaine	Sadeghipour, (2020)
Cd	Wheat (Triticum)	Salicylic acid	Gul et al. (2020)
Al	Barley (Hordeum vulgare)	Ascorbic acid and Salicylic acid	Shahnawaz & Sanadhya (2017)

Table 2. Representative studies on the role of plant growth regulators on different plants exposed to heavy metal stress

HMS	Plants	PGR (Phytohormone)	Mitigation Effects by PGRs	References
Co	Grey mangrove (Avicennia marina)	Jasmonic acid (1, 10 µM)	JA efficiently reduced the accumulation of Cd in leaves.	Yan et al. (2015)
Cd	Faba bean (Vicia faba L.)	Jasmonic acid (JA)	JA alleviate the undesirable impacts of Cd stress by preventing the accumulation of Cd	Ahmad et al. (2017)
Ni	Alyssum inflatum Náyr	Salicylic acid (0, 50, 200µM), jasmonic acid (0, 5, 10 µM)	SA and JA showed ROS detoxification in plant exposed to Ni stress.	Kakavand et al. (2019)
Pb	Brassica campestris	Salicylic acid (SA)	Application of SA improve the growth and yield of the plant by regulating the antioxidant defense system	Hasanuzzaman et al. (2019)
Cd and Zn	Virginia saltmarsh mallow (Kosteletzkya pentacarpos)	Cytokinin (10 µM)	Increased resistance to heavy metals	Zhou et al. (2019)
Cd	Lettuce (Lactuca sativa L.)	Abscisic acid (ABA)	exogenous ABA increases the biomass, photosynthesis and activities of antioxidant enzymes under stressful conditions	Dawuda et al. (2020)
Cd	Maize (Zea mays L.)	Salicylic acid (SA)	Exogenous SA improved the process of photosynthesis and reduce the oxidative damaged occurred under Cd stress	El Dakak and Hassan (2020)
Pb	Triticum aestivum L.	Salicylic acid (SA)	SA application considerably reduced the effect of Pb and improve the amount of biochemical traits of T. aestivum L.	Gillani et al (2021)
Cd	Bean (Phaseolus vulgaris L.)	Salicylic acid (SA)	Foliar applıcatıon of SA allevıate cd-encouraged ROS, methylglyoxal along with lipid peroxidation	Hediji et al. (2021)
Cd	Vigna radiata L	Gibberellins (GAs)	Application GA improve the plant metabolism, enhance the photosynthetic pigments under Cd stress	Hakla et al. (2021)
Cd	Tomato	Salicylic acid (SA)	Exogenous SA reduced the uptake of Cd in tomato plants and its subcellular cells	Jia et al (2021)

PGR:Plant Growth Regulators

Microorganism

Mitigation of metal stress is essential for the conservation and protection of the contaminated soil. Biological methods for the removal of harmful toxic metals are considered as environmentally friendly, cost effective and natural. Use of beneficial microbes for the mitigation of heavy metal stress is one such method. The use of microbes is a very effective bioremediation method in the context of global climate change and the overuse of different fertilizers in soils (Tiwari et al., 2016). Microbes have the potential to survive adverse environmental stresses (Ma et al., 2016b). Rhizosphere soil is crucial territory for various microbes including bacteria, protozoa, fungi and algae. They enjoy a variety of associations with plant species (Zubair et al., 2016). Being an imperative component of the soil, become an essential part of the agricultural production system once the seed comes in to the soil to start a new cycle of life. Microorganisms form a symbiotic relationship with plants. This symbiotic relationship offers ultimate support to the plants in attaining a significant tolerance against heavy metal stress and gaining the essential nutrients (Turner et al., 2013a).

Rhizosphere microorganism has the capacity to degrade the organic and inorganic contaminants via transformation, volatilization, and rhizo degradation (Ullah et al., 2015b). Microorganisms also improve the bioavailability of heavy metals through acidification, chelation, and precipitation. Organic acid released from the microbes pay the way for the sequestration of different metal ions by lowering the pH of soil (Mishra et al., 2017). Oxalic, malic, acetic and gluconic acid are primarily testified for heavy metal solubilization through soil microbes (Gube, 2016). Microbes can easily metabolize the metal ions and obtain energy via oxidation/reduction process (Sathendra et al., 2018). Bacterial strains are widely used for the mitigation of heavy metal stress. Bacterial communities mitigate the heavy metal stress through immobilizing, uptake, mobilizing and transforming the metals ions effectively (Hassan et al., 2017). Different plant growth-promoting rhizobacteria (PGPR) resides around plant root area and positively improve plant growth via facilitating and supplying sufficient amount of nutrient from soil (Nadeem et al., 2014). These (PGP) bacteria have different approaches for the successive metal tolerance, including precipitation, bioaccumulation, biosorption and exclusion in both external and intercellular spaces (Glick, 2010).

Table 3. List of plant-associated microbes reported for plant growth promotion under heavy metal stress (2019 onward)

HMS	Microorganism	Plants	References
Ld	Trichoderma	Mustard	Yaman and Mehta, (2019)
As	Bradyrhizobium japonicum E109 and Azospirillum brasilense Az39	Soybeans	Armendariz et al. (2019)
Cd	Bacillus cereus M4	Oryza sativa L.	Wang et al. (2019b)
Cd	Bacillus cereus strain, ALT1	Soybean	Sahile et al. (2019)
Cd	Rhizophagus clarus	Maize (Zea mays)	Rafique et al. (2019)
Cd	Pseudomonas	Sulla coronaria	Chiboub et al. (2020)
Hg	Pseudomonas putida	Turnip	Alsaleh et al. (2020)
Cr	Staphylococcus aureus strain K1	Wheat	Zeng et al. (2020)
As	Ochrobactrum tritici	Rice	Moens et al. (2020)
Cu	Paenibacillus polymyxa and Bacillus circulans	Maize	Abdel Latef et al. (2020)
Cu	Bacillus sp. 5O5Y11	Zea mays	Esertaş et al. (2020)
Cr	Bradyrhizobium japonicum EI09	Capsicum annum	Nemat et al. (2020)
Pb	Trichoderma asperellum SD-5	Perennial ryegrass	Sun et al. (2020)
Cd	Pseudomonas TCd-1	Rice (Oryza sativa L.)	Wang et al. (2021)
Cu	Pseudomonas lurida strain EOO26	Helianthus annuus L.	Kumar et al. (2021a)
Cd	Azospirillum brasilense Az39	Wheat	Vázquez et al. (2021)
Cd, Pb	Aspergillus niger and Penicillium chrysosporium	Vicia faba L.	El-Mahdy et al. (2021)
Zn	Lysinibacillus	Maize (Zea mays L.)	Jinal et al. (2021)
Cd, Cr	Aspergillus niger	Tomato	Hamayun et al. (2021)
Hg	Aspergillus sp. A31 and Curvularia geniculata P1	Oryza sativa L.	de Siqueira et al. (2021)
Cd, Cr	Aspergillus flavus	Solanum lycopersicum	Hamayun et al. (2021)
Cd	Aspergillus niger TL-F2 and Aspergillus flavus TL-F3	Rygegrass	Fan et al. (2021)
Cd	Pseudomonas sp. K32	Rice seedling	Pramanik et al. 2021
Pb	Bacillus cereus	Pistia stratiotes and Eichhornia crassipes	Zahari et al. (2021)
Cr	Bacillus cereus	Brassica nigra L.	Akhtar et al. (2021)
Cd	Pseudomonas sp. K32	Rice seedling	Pramanik et al. (2021)
Pb	Pseudomonas gessardii BLP141	Sunflower	Raza Altaf et al., (2021)

Table 4. Heavy metal tolerance enhancement in plants through the application of nanoparticles

HMS	NPs	Concentrations	Plant Studied	Impact	References
Cd	ZnO-NPs	(0, 50, 75, 100 mg/L)	Rice (Oryza sativa L.)	Reduced the Cd accumulation in plant	Ali et al. (2019)
Cd	Fe-NPs	(0, 5, 10, 15, 20 ppm)	Wheat	Increased chlorophyll contents and gas exchange attributes in plant	Hussain et al. (2019)
Cd, Pb	ZnO-NPs	(100 mg/L)	Lettuce (Lactuca sativa L. var. Longifolia	ZnO NPs significantly reduced the accumulation of Cd and Pb in roots and shoots of the plant	Sharifan et al. (2019)
Cd	ZnO-NPs	(50, 100, 500 mg/kg)	Rice (Oryza sativa L.)	ZnO-NPs could improve plant growth, especially in the early-growth stage, and alleviate the toxic effects of Cd	Zhang et al. (2019)
Cd	TiO_2-NPs	(0, 100, 250 mg/L)	Maize (Zea mays L.)	It remarkably reduces the accumulation of Cd in plant	Lian et al. (2020)
Co	Co_3O_4-NPs	Co_3O_4 NPs (0, 50, 100, 250, 500, 1000, 2000, 4000 mg L^{-1})	Brassica napus L.	Co_3O_4-NPs showed positive effect on growth and antioxidant system of the plant	Jahani et al. (2020)
Cr	Cu NPs	(0, 25, 50, 100 mg kg^{-1} of soil)	Wheat	Decrease the cellular oxidative stress and improve the plant growth	Noman et al. (2020)
As	Nano-TiO_2	(0, 10, 100, 1000 mg/L)	Rice (Oryza sativa L.)	Nano-TiO_2 amendment notably alleviated oxidative stress resulting from arsenic exposure	Wu et al. (2021)
As	MgO-NPs	(200 mg kg^{-1})	Rice (Oryza sativa L.)	MgO-NPs decreased the ROS and inhibited arsenic translocation in rice plants	Ahmed et al. (2021)
Cd	FeO-NPs	(0, 25, 50, 100 mg/kg)	Wheat	Iron oxide nanoparticles ameliorated the cadmium and salinity stresses in wheat, facilitating photosynthetic pigments and restricting cadmium uptake	Manzoor et al. (2021)
Cd	TiO_2-NPs	(100 mg/L)	Wheat	TiO_2-NPs significantly decreased Cd in wheat straw, roots, and grain	Irshad et al. (2021)
Cu	TiO_2-NPs	(1, 2, 5, 20 mg/L)	Soybean (Glycine max L.)	TiO_2-NPs improve growth and restricts the bio-availability of Cu	Xiao et al. (2021)
Cd	SiO_2-NPs	SiO_2 NPs (100, 200 µM	Moso bamboo	Silicon nanoparticles improve the seedling growth and seedling biomass under Cr stress.	Emamverdian et al. (2021)
Hg	S-NPs	(300 mg/L)	Brassica napus L.	Sulfur (SNPs) alleviated Hg-induced oxidative stress and improved plant growth	Yuan et al. (2021)
Pb	MgO-NPs	(5 mmol/L)	Wild carrot (Daucus carota)	Magnesium oxide nanoparticles detoxified ROS to mitigate Pb stress and improved the growth of plants	Faiz et al. (2021)
Cu	ZnO-NPs	(50 mg/L)	Tomato	ZnO-NPs promoted photosynthetic capacity by enhancing antioxidant activities leading to ROS scavenging.	Faizan et al. (2021)
As	Fe_3O_4-NPs	(5, 10, 15 ppm)	Rice (Oryza sativa L.)	Fe_3O_4-NPs alleviated the arsenic stress and enhanced the plant growth.	Khan et al. (2021)
As	ZnO-NPs	(25 ppm)	Wheat	ZnO-NPs increased germination percentage, shoot and root growth, chlorophyll, carotenoid, RWC, MSI and protein content.	Kumar et al. (2021b)
As	Fe-NPs	(0, 25, 50 mg/L)	Rice (Oryza sativa)	Fe-NPs reduced the as phytotoxicity by increasing the content of chelating agents (proline, GSH and PCs	Bidi et al. (2021)
Cd	TiO_2-NPs	(0, 40, 80, 160 mg/L)	Coriandrum sativum L.	TiO_2-NPs treated seedlings exhibited reduced Cd contents besides improved agronomic traits (seedlings biomass, number of seeds and yield.	Sardar et al. (2021)

Bacterial population in excessively metal contaminated soil primarily comprises of Proteobacteria, Firmicutes and Actinobacteria. While most prominent genera include *Arthrobacter, Bacillus and Pseudomonas* (Pires et al., 2017). Similarly filamentous fungi genera including Penicillium, Trichoderma, Mucor and Aspergillus are widely recognized for their effective role in remediation of heavy metal stress (İkram et al., 2018; Sun et al., 2020; El-Mahdy et al., 2021; Li et al., 2021). Cell wall of fungi possess excellent metal binding characteristics owing to the presence of negatively charged functional groups including sulfhydryl, amine, and carboxylic in wall components (Ong and Ho, 2017). Arbuscular mycorrhizal fungi (AMF) are also admirable soil microorganism reported in heavy metal stress tolerance. They develop a direct physical linkage between the plant root and soil, which in turn increases the surface area of root enabling the nutrients and mineral absorption by various plants species (Saxena et al., 2017). AM fungi are also actively involved in the mitigation of heavy metal stress in different plants as reported in various studies (Cantamessa et al., 2020; Hao et al., 2021; Zhang and Chen, 2021). At this point, we have gathered a list of newly published research studies depicting the successful implementation of plant-microbes association for the effective mitigation of metal stress in various plants in Table 3.

Nanoparticles

Nanotechnology is performing a substantial role in addressing an immense array of environmental complications by providing effective and advanced solutions. Heavy metal pollution has gained huge consideration due to their ever-increasing concentration in the environment. Unique physiochemical properties of nanoparticles (NPs) make them extremely effective for the remediation of heavy metal stress (Zhou et al., 2021). Nanoparticles (NPs) are tiny units with a size of 1-100 nm in range (Sachdev and Ahmad, 2021). In comparison to the other ordinary materials, NPs possess several advantages including decent catalytic proficiency, extra added surface reaction site and high surface activity along with other exclusive magnetic and optical properties (Yang et al., 2018; Wang et al., 2019), making them a favorable technology for endorsing plant productivity and growth (Mostamed et al., 2019). Nanoparticles (NPs) are efficaciously applied in agriculture sector for the sustainable production of crops worldwide (Gandhi, 2021). Nanotechnology showed a great opportunity to increase the crop yield and its protection and thus resolved some of the major challenges that are currently encountered in agriculture (Neysanian et al., 2020).

Nanoparticles are also remarkably being examined in the field of green agriculture, particularly in linked with the plant growth. Nanoparticles are effectually involved in the regulation of oxidative stress in various plants (Sachdev and Ahmad, 2021). Nanoparticles could effortlessly improve plant growth, seed germination, increase rate of photosynthesis, mitigate oxidative stress, regulating gene expression, promoting nutrition balance, improving productivity, and crop yield as re-ported in previous studies (Kah et al., 2019; Neysanian et al., 2020; Rai and Jajoo, 2021). Then again, NPs are also utilized as nano pesticides and nano fertilizers (Muhammad et al., 2020; Rehmanullah et al., 2020; Fatima et al., 2021). On the other hand, wide range of NPs including titanium oxide (nTiO_2), aluminum oxide (nAl_2O_3), zinc oxide (nZnO), silicon dioxide (nSiO_2), copper oxide (nCuO), cerium dioxide (nCeO_2), magnetite (nFe_3O_4) and carbon nanotubes (CNTs) have shown tremendous potential towards plant growth promotion, scavenging of (ROS), enhancing the activities of antioxidant enzymes, mitigating the plant stress, improving quality and yield of the crop (Usman et al., 2020; Wang et al., 2021).

Past decade has received incredible contribution from nanoparticles in improving the soil characteristics and plant growth, specifically in the management of soil contaminated by heavy metals (Tripathi et al., 2015; Li et al., 2016; Hussain et al., 2018; Rizwan et al., 2019; Lian et al., 2020; Adrees et al., 2021). NPs usually accumulate in plant's cell wall, where they bind themselves with heavy metals and form different complexes. These complexes adsorbed on cell surface, thereby impeding the active migration of heavy metals in plant tissues. Nanoparticles effectively absorb and transform the heavy metals in soil by limiting the bioavailability and mobility of these toxic heavy metals. For example, Yue et al. (2021) reported that Nano-iron materials transform the arsenic and stabilizes it in soil. Amendment of Cu-NPs showed significant reduction in the translocation of Cr from roots to shoots of the wheat plant through effectively immobilizing the Cr in soil, thereby supporting plant growth by dismissing severe cellular oxidative stress (Noman et al., 2020). Similarly, amendment of meta-sodium silicate significantly reduced the bioavailability of lead (Pb) and decreased the accumulation of Pb in brown rice via increasing the sorption of Pb onto ferrihydrite and effective precipitation of $PbSiO_3$ in soil (Zhao et al., 2017). NPs increase the defense capacity of plant by regulating the transport genes involved in the transport of heavy metals. Nanoparticles improve soil strength, it decreases compressibility and permeability of soil (Taipodia et al., 2011). NPs effectively improve the antioxidant system of the plant via magnificently mitigating the oxidative damage through scavenging the (ROS), which ultimate increases the growth, yield and nutritional content of the plant. García-López et al. (2018) reported that application of zinc oxide nanoparticles significantly improves the activity of antioxidant enzymes, such as activities of POD, APX and CAT were considerably improving by 2.3 at 400 mg L^{-1} of ZnO NPs, 4 500 mg L^{-1} ZnO NPs and 6.4 folds 500 mg L^{-1} ZnO NPs respectively in *Capsicum chinense*. Different studies suggests that nanoparticles ameliorate the harmful effects of heavy metals by immobilization of heavy metals (Azeez et al., 2019; Lin et al., 2019), restricting the accumulation of heavy metals (Manzoor et al., 2021) improvement performance of photosynthetic pigments (Rai-Kalal and Jajoo, 2021), mitigation of oxidative stress (Rizwan et al., 2019; Yuan et al., 2021) and improving the growth under heavy metal stress (Fatima et al., 2021). The fruitful contribution of nanoparticles (NPs) in incapacitating challenges of heavy metal induced toxicity has been reported by different investigators globally as given in Table 4.

Conclusions

Metals such as aluminium, cobalt and chromium at low concentrations are essential for plant growth but cause toxic effects to the environment and plants at higher concentrations. The first way to tolerate heavy metals in plants is avoidance and the second way is resistance. When plants are exposed to heavy and toxic metals, they developed various detoxification mechanisms to minimize harmful effects. Metal tolerance in plants depends on biological, chemical, and physiological adaptations. Other practices including seed priming, active involvement of plant growth regulator, use of osmoprotectants, successful plant microbes' crosstalk, and recent utilization of nanoparticles are worth using strategies in mitigation of heavy metal stress in plants. These practices effectively regulate the activities of antioxidant enzymes for the alleviation of heavy metal stress in plants, creditably improving the plant tolerance via preserving cell homeostasis and amending the adversative effects of heavy metal stress in plants. These inventive strategies offer an enriched understanding of how to boost crop productivity under heavy metal stress in order to decrease the risk to global food security.

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